REVIEW OF *PERAMUS TENUIROSTRIS* OWEN (EUPANTOTHERIA, MAMMALIA)

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BY

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REVIEW OF *PERAMUS TENUIROSTRIS* OWEN (EUPANTOTHERIA, MAMMALIA)

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SYNOPSIS

Review of *Peramus tenuirostris* Owen (Eupantotheria, Peramuridae) was occasioned by the discovery of a fragmentary maxilla, B.M.(N.H.) M21887, containing part of the hitherto undescribed upper dentition. M^2 and M^3 of this fossil have large paracones and metacones, small stylocones, and lingual cingula but lack distinct protocones. M^1 lacks a stylocone and the metacone does not have the typical tribosphenic functions. A lingual cingulum is not developed. The four premolars are two-rooted and have trenchant crowns. M^4, the terminal molar, was destroyed during fossilization. G. G. Simpson's (1928) catalogue and description of the mandible of *Peramus* are revised.

Peramus probably is a descendant of the Rhaetic mammal *Kuehneotherium*, but *Amphitherium* is not one of the members of this lineage. *Aegialodon* from the English Wealden could be a descendant of *Peramus*. *Pappotherium* and *Holoclemensia* from the Albian, Trinity Sands of North America probably include a peramurid other than *Peramus* in their late Jurassic ancestry.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The entire sample of *Peramus tenuirostris* Owen, family Peramuridae, is now preserved in the collections of the Department of Palaeontology, British Museum (Natural History). All these fossils are part of the S. H. Beckles collection from Purbeckian strata exposed at Durlston Bay, Dorset. Since publication of G. G. Simpson's catalogue (1928) the sample has been significantly augmented in both

size and scientific value. In this paper his catalogue is brought up to date, two specimens of *Peramus tenuirostris* that recently have been thoroughly prepared are described, and some interpretations of dental function and phylogenetic relationships of the genus are presented.

Several years ago while studying the collections of Purbeckian reptiles in the British Museum (Natural History), Dr. Robert Hoffstetter (1967) found four partially prepared fossils from the Mammal Bed that he suspected to be mammalian remains. Additional preparation verified his suspicions. One of these is a mandible, M21885, containing an incisor, a larger tooth of caniniform morphology, and fragments of postcanine teeth. This fossil, which was formerly catalogued under number 48255, is certainly part of the lower jaw of a mammal, but a more specific identification cannot be made. Three mammalian fossils were found in a group of specimens numbered 48407. One, M21886, is a fragment of mandible containing two molars that is now identified as *Amblotherium* sp. The second, M21887, is the fragment of maxilla of *Peramus tenuirostris* described subsequently. The third, M21888, is a fragmentary mandible of *P. tenuirostris* that has been described elsewhere (Mills 1964).

The research reported here reflects the encouragement and help of a large number of colleagues. Dr. Errol I. White, former Keeper of the Department of Palaeontology, and Dr. A. J. Sutcliffe initially suggested that the sample of *Peramus tenuirostris* be restudied and made the material available. They and Dr. H. W. Ball, Keeper of Palaeontology, have supported this study in a variety of significant ways. Their contributions are gratefully acknowledged.

As the specimens of *Peramus* were prepared and became available for study, they have been seen by many palaeontologists. A paper including a description of M21888 has been published (Mills 1964). Drs. K. A. Kermack and J. R. E. Mills started to prepare a report on the maxilla, M21887, but the press of other responsibilities kept it from completion. When a Natural Science Foundation Postdoctoral Fellowship made it possible for W. A. Clemens to return to England, he was invited to take part in the study. Dr. Kermack withdrew, however he not only made his preliminary notes and photographs available, but also Prof. M. Abercrombie and he provided research facilities in the Department of Zoology, University College, London.

The conclusions presented here embody the results of interchanges of ideas with many other palaeontologists. Although not committing them to the interpretations given subsequently, we wish to acknowledge the valuable, long discussions with Prof. P. M. Butler, Prof. A. W. Crompton, Dr. K. A. Kermack, Dr. B. Krebs, Prof. A. W. Kühne and Mrs. Frances Mussett that have played an important part in their formation.

The fossils described here were skilfully released from the rock by Mr. Arthur Rixon whose deft preparation has added greatly to the value of the collections of *Peramus* and other British Mesozoic mammals. Text-fig. 1 and the plates are the work of Mr. A. J. Lee. The cost of preparation of these illustrations was met through a grant from the Museum of Paleontology, University of California, Berkeley.

II. TAXONOMY AND MATERIAL

The synonymies of *Peramus tenuirostris* Owen given by Simpson (1928, p. 121) have not been modified. The following additions are made to his catalogue of material (*ibid.*, pp. 121–122):

47742. None [Holotype].
47739. Removed from rock and cleaned by A. Rixon in 1968; redescribed here.
47744. Removed from rock and cleaned by A. Rixon in 1962; described by J. R. E. Mills (1964).
47751. None.
47754. None.
47799. None.
48404. Removed from rock and cleaned by A. Rixon in 1962; described by J. R. E. Mills (1964).
M21887. Left maxilla with eight fragmentary postcanine teeth. Removed from rock and cleaned by A. Rixon in 1961; described here.
M21888. Right mandible with M_3, trigonid of M_4 and fragments of P_3 through M_2. Removed from rock and cleaned by A. Rixon in 1962; described by J. R. E. Mills (1964).

As far as can be determined from the records all these fossils came from the Mammal Bed, one of the units of the Purbeck beds exposed in the cliffs at Durlston (=Durdlestone) Bay. The Mammal Bed is stratigraphically below the Cinder Bed and part of the Lulworth Beds (Casey, 1963). Problems of determination of the age of the Lulworth Beds have been reviewed by Dodson *et al.* (1964). Because the Purbeckian mammals have long been described as being of late Jurassic age and a change in terminology to reflect the disparity of standards has no apparent value in the context of this paper, the Boreal standard for the Jurassic–Cretaceous boundary and a late Jurassic age for the Purbeckian mammals are employed. Purbeckian is used in the sense suggested in the report by Ager (1963), ". . . not a stage but a facies, predominantly fresh-water and continental . . .".

III. DESCRIPTIONS AND INTRAGENERIC COMPARISONS

a. *Maxilla*, B.M.(N.H.) M21887

In addition to lateral displacement, the fossil (Pls 1 and 2) was distorted by pressure from a posterior direction that crushed or severely damaged the distal three molars. A groove along its dorsal edge above these molars (Pl. 1, fig. 1) might mark the course of a maxilla-jugal suture. Otherwise no clear evidence of bones other than the maxilla was found in M21887. An anteroposteriorly elongated trench dorsal to P^4 and M^1 probably marks the course of a collapsed infraorbital canal with its foramen dorsal to P^3 and P^4.

Eight teeth in various states of preservation are present. Part of the root of a tooth immediately mesial to the first preserved premolar (Pl. 1, fig. 1) shows these teeth were not separated by a long diastem. The lingual and distal sides of the alveolus of this more mesial tooth and the fragment of its root suggest the tooth was large, single-rooted, and caniniform. Curvature of the maxilla and absence of

evidence of alveoli suggests the dentition lacked additional distal elements. Thus the fossil probably contains the remains of the entire postcanine dentition. The postcanine dental formula proposed by Simpson (1928) for the lower dentition of *Peramus*, four premolars and four molars, is adopted here.

All premolars are two rooted and their crowns have a basic trenchant morphology. The crown of P^1 is broken from its roots and displaced buccally. Its apex is slightly in advance of the center of the crown. No evidence of basal accessory cusps or cingula was found.

The crown of P^2 is displaced buccally and slightly mesially to overlap the distal end of P^1. Unlike P^1, the fracture is closer to the apex of the crown and cuts across the region where basal cusps or cingula would be expected. Probably a small posterior basal cusp was present and its remains are not now clearly distinguishable among the fragments along the zone of fracture. However, the step on the distal margin of P^2 might only be an artifact of mesial displacement of the crown. Otherwise no evidence signals the presence of basal cusps or cingula. P^2 has the appearance of being slightly smaller than P^1 but damage at the crown's base prevents accurate measurement of comparable dimensions.

The position of their roots suggests P^{1-2} were not separated by a diastem. A major fracture zone crosses the fossil posterior to P^2. Movement associated with this fracturing displaced the anterior part of the maxilla posteroventrally with a slight rotation and depression of its anterior end. Before distortion P^2 and P^3 were separated by a small diastem of about the same length as that separating P^3 and P^4.

Although the mode of preservation has muted textural and colour differences between enamel and dentine, the absence of a vitreous surface layer, discernable on other teeth, indicates that enamel has been lost from large parts of the dorsal two-thirds of the crown of P^3. At least a small, posterior basal cusp was present. The roots of P^3, which form an angle of approximately 45 degrees, appear to be much more widely divergent than those of the other premolars. Perhaps the tooth here designated P^3 is a deciduous premolar.

The bone forming the surface of the diastem between P^3 and P^4 is deeply pocketed (Pl. 1, fig. 2). The palatal process of the maxilla is broken and distorted in this region. The pit might be an artifact, but this appears unlikely.

In length and height of crown P^4 is distinctly larger than the other premolars. A nearly horizontal fracture cuts the mesial half of the crown near its base. Loss of enamel along this fracture accentuates the anterior basal cingulum (Pls 1 and 2). The apex of the main cusp is slightly in advance of the midpoint of the crown. Its mesial surface lacks a vertical ridge. Distally a prominent ridge extends from the apex toward the disto-lingual basal cusp. They are separated by only a small notch. Buccal to this ridge the surface of the main cusp is either flat or slightly depressed. A second distal basal cusp of slightly smaller size and more mesial position is situated buccal to the first. A small cingulum extends forward a short distance mesially from the disto-lingual basal cusp. Otherwise the tooth lacks lingual or labial basal cingula.

M^1 is two rooted, the distal root is larger and slightly wider transversely. A high paracone, which is now fractured and displaced at two levels, dominates the crown.

Low on its distal surface is a second major cusp. Identification of this cusp is discussed subsequently (p. 103). M^1 has been moved lingually and mesially, and its mesio-buccal corner damaged. What remains indicates only one small cusp was present. Certainly this part of the crown did not overlap the buccal side of the distal end of P^4. The crest along the mesial edge of the paracone might not have reached the mesio-buccal cusp. Irregularities of the crown's damaged surface suggest the crest was deflected disto-buccally. If it was, this disposition of the crest suggests the mesiobuccal cusp is a parastyle and not a stylocone.

On the lingual surface of M^1, just ventral to the alveolar margin, are vestiges of a narrow cingulum. Mesio-lingually it is represented by a relatively broad shelf carrying two distinct cusps of which the more lingual is also the more dorsally placed. Distally, across the middle of the crown, the cingulum is virtually obsolete being represented only by a line marking an abrupt change in the slope of the lingual surface. On this line are two isolated cusplike expansions. On the most distal quarter of the crown the cingulum again becomes distinct. In this region it curves ventrally to reach a small cusp which lies adjacent to the large cusp at the distal end of the crown. Mesio-bucally from the latter are two stylar cusps. The stylar shelf is continued mesially by a narrow cingulum.

Most of the parastylar region of M^2 is missing, however enough remains to show it was large and overlapped the distal end of M^1. Several approximately horizontal fractures pass through the crown of M^2 but little displacement occurred along most of them. The crown of M^3, acting as a wedge, was driven dorsal to that of M^2 pushing it ventrally and rotating its base distally. Distal displacement appears to be minor and the angle of the embrasure between M^1 and M^2 not greatly distorted. In contrast, the distal lobe of the stylar shelf of M^2 was crushed against the crown of M^3.

From the high paracone of M^2 a ridge sweeps mesio-buccally to a small cusp, the stylocone, immediately adjacent to the missing parastylar region (Pl. 1, fig. 2, and Pl. 2, fig. 2). Two small cuspules are present on what remains of the buccal edge of the anterior lobe of the stylar shelf. The small stylocone is undamaged by post mortem fracturing and can only have been slightly blunted by wear. A short ridge extends mesially from its base. Directly mesial to the ridge linking the stylocone and paracone the crown is gently rounded, not a vertical wall.

Dorsally, near the lingual base of the crown, three cuspules are imperfectly linked to form a cingulum-like ledge (Pl. 2). The metacone of M^2 is high on the side of the paracone. Their common base is separated from the distal lobe of the stylar shelf by a diagonal linear depression, now the locus of a major fracture. Mesial to the paracone of M^3 the crown of M^2 is heavily crushed. The shards remaining are sufficient to be the residue of a cusp the size of that in the comparable position on M^3. Buccal to this crushed area part of the crown of M^2 remains intact but displaced. From a small cusp near the disto-buccal corner a ridge extends toward the crushed area. A groove mesio-buccal to this cusp separates it from what appears to be the remains of one or two smaller cusps. M^2 is supported by three roots of approximately equal size.

Part of the parastylar region of M^3 is also missing but, in comparison to M^2, the fracture is more vertically oriented and situated farther buccally. It cuts through

a cusp, possibly the parastyle, on the buccal side of the crown. A ridge from the stylocone extends disto-buccally toward the edge of the crown but reaches neither the parastylar cusp nor the more distal, small marginal stylar cusps. Relative to this section of the crown the paracone and metacone are displaced mesially. These cusps do not differ in size or position from those of M^2. Although now offset, a low ridge, paracrista, connected the paracone and stylocone.

On the lingual surface of the crown a short, narrow cingulum shows no evidence of subdivision into cusps (Pl. 2). This part of the tooth suffered some damage and is partly obscured by the remains of M^4. Clearly both mesially and lingually no pieces of the crown of M^3 are missing and, except for possible slight distortion or post mortem abrasion, the original shape of the crown and its lingual cingulum is preserved. Distolingually some enamel is missing. Loss of these chips carried away that part of the distal limb of the cingulum not covered by M^4. The curvature of adjacent enamel surfaces does not suggest, but cannot rule out, greater transverse width of the distal part of the lingual cingulum. Probably three roots are present, but they are not clearly visible.

Like M^2, a fracture follows the depression between the common base of paracone and metacone of M^3 and the distal lobe of the stylar shelf, but the latter area is not as heavily damaged. Three cusps are present on this lobe. The most lingual is the highest and largest. Although its apex is higher than the buccal cusp, the middle cusp in the row has the smallest volume.

M^4 bore the brunt of the distorting pressure and its crown is now crushed against M^3. Remains of alveoli prove that at least part of the material is derived from an upper molar. No evidence suggests the presence of parts of a lower molar, but the possibility cannot be ruled out.

The mass of dental material now covering part of the disto-lingual surface of M^3 could be the remains of the major lingual cusp of M^4. The buccal mass of M^4 is not as crushed but was rotated clockwise through approximately 90 degrees. It includes part of the parastylar region carrying the bases of two cusps of subequal size followed distally by two smaller cusps. M^4 was supported by at least a buccal root under the parastylar region and a second lingual root. No indication of a third root was found.

At the time of its death the animal from which M21887 is derived had not lived long enough to heavily wear its dentition. Only one or two surfaces that are clearly the result of wear could be found, for example flat areas on the crests of the ridges radiating from the stylocone of M^2. Planar areas on the disto-lingual surface of the paracones and mesio-lingual surface of the metacones of M^2 and M^3 might be wear facets, but the evidence is not conclusive. Admittedly evidence of wear may now be obscured by a combination of the small size of the fossil, imperfections in preservation of the surfaces of the teeth, and the necessary coat of preservative.

b. *Mandible*, B.M.(N.H.) 47739

The two distal, single-rooted incisors are represented by the broken root of the more mesial and the alveolus of the distal (Text-fig. 1). Dimensions of both alveoli are approximately: length = 0·4 mm., width = 0·3 mm. Although the tip of the

dentary is missing, the curvature of what remains suggests the presence of an additional one or two, if not more incisors in the complete dentition. Before burial the canine was lost. The oval aperture of its alveolus has a length of 1·0 mm. and a maximum width of 0·3 mm. Although its alveolus is slightly constricted medially, the canine was probably supported by a single root.

The distal margin of the crown of P_1 is slightly concave and slopes down to the single posterior basal cusp. Probably P_1, like P_2 and P_3, lacked an anterior basal cusp, but this area of the crown is damaged. There is no indication of a lingual or buccal basal cingulum. All premolars are two rooted (Pls 3 and 4).

Other than its slightly larger overall size and relatively larger posterior accessory cusp, P_2 is very similar to P_1. On the buccal side of the dentary a mental foramen is present below and slightly in advance of the anterior root of P_2. P_3 illustrates the mesio-distal trends for gradual increase in premolar size and increase in relative size of the posterior basal cusp.

P_4 is distinctly larger and higher than P_3. It also differs in the presence of a small anterior basal cusp just lingual to the midline of the crown. From the apex of the main cusp a crest on its lingual side curves buccally onto the damaged dorsal surface of the talonid-like posterior basal cusp. What remains suggests this crest extended directly to the apex of a single cusp. There is no evidence of a metaconid or distinct talonid basin on either side of the crest.

M_1 is neither as long nor as high as P_4. Its largest cusp, the protoconid, has a flat lingual and convex buccal surface. Two small cusps are present on the mesial end of the crown. The smaller is situated just in front of and in line with the lingual side of the protoconid. A larger cusp (anterior cusp of Mills 1964), its apex now missing, was present directly lingual to it. Possibly a third cusp was present buccal to the first at a point where a small, oval scar indicates a flake of enamel was chipped away (Pl. 4, fig. 1). M_1 lacks a large, projecting metaconid of the kind found on the following molars. However, the distal slope of its protoconid is drawn out into a blade. Buccal and lingual grooves on the crown vaguely demark the bodies of the protoconid and metaconid. The tip of the metaconid is now broken away but the fracture surface indicates that it had a small, separate apex. The crest along the distal edge of the metaconid is separated by a notch from the crest of the talonid cusp. Apparently there was only one talonid cusp set slightly lingual to the midline, but its apex is missing and the possibility of the presence of two, very closely approximated cusps cannot be excluded. Lingually and buccally from this crest the crown falls away gradually toward the nearly vertical sides of the talonid. An entoconid is lacking. Slight bevelling of the buccal side of the talonid is probably the first stage in development of a wear facet resulting from contact with the paracone. No evidence of wear was found on the lingual side of the talonid. A mental foramen is present beneath and between the adjacent roots of P_4 and M_1.

Unlike M_1, M_2 has a high, three-cusped trigonid. Its protoconid is distinctly higher than the paraconid. The latter is closer to the midline than the larger and more lingually situated metaconid. The edge of the crown extends mesially to contact the back of M_1. Enamel is missing from both the lingual and buccal sides of the mesial end of the trigonid. Basal cusps serially homologous to those of M_3

and M_4 might have been present. A prominent crista sweeps down from the metaconid to a low point at the base of the hypoconid distal to the embrasure that received the paracone. This crest forms a prominent vertical "lip" on the back of the trigonid (Mills 1964). The surface of the embrasure between protoconid and hypoconid was scarred during early preparation and, if any existed, clear traces of wear cannot now be recognized. At the end of the crown, distal and lingual to the hypoconid, is a much smaller and lower hypoconulid. A very shallow trough starting between these cusps and paralleling the crista obliqua, descends linguomesially across the lingual face of the talonid. A small cusp is present in the position of an entoconid.

M_2 and M_3 were probably very similar in size and morphology, the major differences now distinguishing them appear to be the result of post mortem damage. M_3 has two prominent anterior basal cusps; the lingual is awl-like and directed mesiodorsally. The buccal anterior basal cusp, now slightly blunted, is in a more ventral position and merges with an expansion extending toward the buccal base of the protoconid. The hypoconulid of M_3, which is situated between the anterior basal cusps of M_4, is slightly larger and extends farther distally than that of M_2.

The trigonid of M_4 does not exhibit any significant differences from that of M_3. Its buccal anterior basal cusp is better preserved and clearly illustrates union with the expansion across the base of the protoconid. In contrast, the talonid of M_4 most closely resembles that of M_1 in its narrower, ridge-like morphology and presence of only one major cusp. Unlike M_1, a small entoconid is present and the talonid crest is directed posterobuccally.

Mesially (Text-fig. 1) the masseteric fossa terminates in a distinct pocket. Ventrolaterally the concave floor of this fossa continues onto the convex side of the horizontal ramus without interruption by a pocket or a ridge. On the lingual side of the dentary the slope of the dorsal surface of the symphysis is continued posteriorly along the horizontal ramus to the level of M_1 by a line reflecting a change in curvature of the ramus. Slightly posterior to the level of M_4 a well defined groove begins and extends to the posterior end of the specimen. This groove first lies beneath the anterior part of the pterygoid fossa and then merges with it. The fragments of bone preserved in 47739 give no evidence of a dental foramen. Also there is no evidence clearly suggesting the presence of a coronoid.

TABLE 1

Measurements, B.M.(N.H.) 47739, in millimetres

	Length	Width
P_1	·52	·24
P_2	·66	·27
P_3	ca. ·7	—
P_4	·96	·36
M_1	·93	·40
M_2	1·0	·51
M_3	1·0	·47
M_4	·91	·47

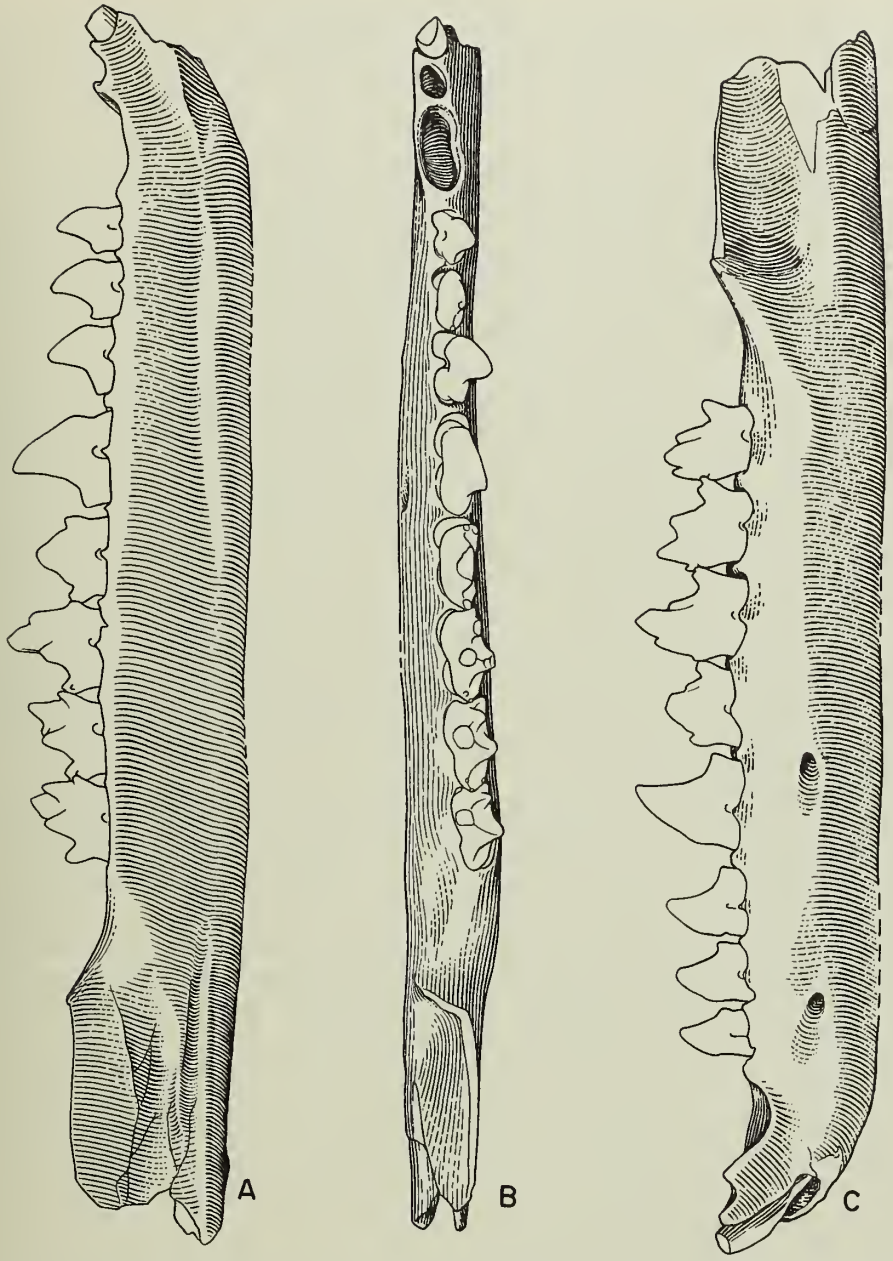

FIG. 1. *Peramus tenuirostris* Owen. × 13. Mandible, B.M.(N.H.) 47739, with fragment of root of an incisor (I_3?), alveoli of distal incisor and canine, P_{1-4} and M_{1-4} (teeth outlined, see pls 3 and 4) in A, lingual view, B, occlusal view, and C, labial view.

c. *Other Mandibles*, Excepting B.M.(N.H.) 47799 and 48404

The presence of at least four lower incisors is demonstrated by 47744 in which three incisors are represented by alveoli and a fourth (probably I_2), a procumbent peg-shaped tooth, is preserved (note Mills 1964, p. 118). Probably only four lower incisors were present but none of the available mandibles clearly rules out the presence of additional teeth anteriorly.

Although slightly constricted medially the canine alveolus of 47739 (Text-fig. 1) is clearly one that housed a single-rooted tooth. Mills (1964, p. 118), on the basis of the morphology of M21888 and 47744 thought the canine of *Peramus* was two rooted. The canine region of 47744 is crushed and fragments of bone are missing from one side of the ramus. The parts preserved suggest the tooth was either two-rooted or had a single root with a deep vertical medial constriction.

Reinterpretation of M21888 in light of comparisons with 47739 results in identifications of the teeth preserved differing from those published earlier (Mills 1964). The most distal preserved molar, only its trigonid remains, is probably M_4. M_3 is the most complete molar preserved in the jaw. M_2 and M_1 are represented by the bases of their crowns and talonid regions. P_4 is similarly damaged but more of the crown of P_3, which is the most mesial tooth in M21888, is preserved. By this interpretation the posterior mental foramen of M21888, like 47739, lies beneath and slightly anterior to the mesial half of M_1.

None of the anterior premolars, P_1 through P_3, preserved in these mandibles have a distinct anterior basal cusp. Some show a slight swelling on their mesio-buccal slope, the region of the "antero-buccal ledge" in the terminology of Butler (1939). The P_3 of M21888 was mistakenly thought to be a geminated tooth (Mills 1964, p. 119). Comparisons with the subsequently cleaned 47739 indicate abnormal development did not take place.

P_4 of M21888 has lost its main cusp but the posterior basal cusp remains. The curvature of the fracture surface indicates a small cusp might have been present lingual and mesial to the posterior basal cusp. P_4's of both 47744 and 47754 are damaged. What remains of their crowns does not differ from that of 47739.

M_1 of the holotype, 47742, closely resembles the first molar of 47739. It differs in lacking the pronounced flattening of the lingual side of the protoconid. Also only one prominent anterior basal cusp is present slightly lingual to the midline of the crown, but a basal mesial cingulum continues across the crown to the buccal side. The talonid is broad and dominated by a single cusp. Because of a covering of matrix, presence or absence of an entoconid cannot be determined.

In comparison to the adjacent teeth, M_1 of 47744 is relatively small. The area mesial to its protoconid is broken and distortion may be masked by a thick layer of preservative. Its talonid is short (mesio-distally), narrow and unicuspid. The metaconid is not well defined. Like the M_1 of 47742 the protoconid lacks the flattening of its lingual surface found in 47739.

The first molars of 47751 and M21888 are damaged. As far as can be determined M_1 of 47751 does not differ significantly from that of 47739 except in the presence of a minute entoconid. M_1 of M21888 is larger, relative to the adjacent teeth, than that of 47739. The lingual anterior basal cusp and the buccally directed cingulum

of M21888 resemble those of 47742. The distal face of the protoconid is broad and expanded buccally, thus resembling the posterior molars more than is the case in 47739. A small cusp on the distal face of the trigonid might be the metaconid but it could be a posterior accessory cusp comparable to those found on the molars of 47799 and 48404.

Recognizing the points of difference, probably reflecting individual variation, the M_1's of 47739, 47742, 47744, 47751, and M21888 conform to a morphological pattern that clearly distinguishes them from the more distal molars. If present, the metaconid is only a small projection on the distal slope of the protoconid. None of the M_1's have a paraconid, although one of the anterior basal cusps might be its remnant or precursor. Excepting the minute entoconids present on some M_1's, their talonids are unicuspid. The crest of the talonid is directed distally or distolingually and lacks a prominent buccal expansion.

The mesial end of M_2 of 47739 is damaged and presence of anterior basal cusps cannot be verified. Morphology of M_2's of 47742, 47744, 47751, and M21888 indicates that two anterior basal cusps can be present. These are situated on either side of the midline; the intervening depression received the distal end of M_1. The lingual basal cusp (anterior cusp, Mills 1964) is larger and in a more dorsal position than the buccal (antero-buccal ledge, *ibid.*). Mills (*ibid.*) has described the variation in structure of the trigonid of M_2 and the "lipping" produced by the high ridge extending down the distal face of the trigonid.

The talonid of M_2 of M21888 is damaged but certainly its hypoconid did not project as far buccally as that of 47739. A wear facet on the anterior buccal basal cusp of M_3 of M21888 is aligned with the wear facet produced by the paracone of M^2 on the talonid of M_2. Perhaps in this animal a re-entrant to receive a metacone was not present. To the extent that they are preserved and prepared the talonids of the M_2's of 47742, 47744, and 47751 do not differ significantly from that of 47739. The crest along the distal face of their trigonids extends posterobuccally to a hypoconid and then turns posterolingually to reach a smaller hypoconulid thus producing a small but distinct buccal salient. A minute entoconid is present on at least some M_2's.

M_3's preserved in 47742, 47751 and M21888 do not differ significantly from that of 47739. On all the talonid is dominated by the hypoconulid and slightly higher, buccally salient hypoconid. Mills (1964, p. 120) has described the few differences between M_2 and M_3. The talonid of M_4 of 47742 is relatively shorter (mesiodistally) than that of M_4 of 47739. Although partly obscured by rock, it also appears to be dominated by a single cusp.

Krebs (1969) called attention to the presence of a rudimentary coronoid on the lower jaws of certain dryolestid and paurodont eupantotheres. Traces of a coronoid or a coronoid-dentary suture are not apparent on 47739. However, small triangular, rugose areas near the anteroventral corners of the pterygoid fossae of 47751 and 47754 might indicate the presence of coronoids in these individuals of *Peramus*.

d. *Mandibles*, B.M.(N.H.) 47799 and 48404

These two mandibles are described separately for they consistently differ from the

others in one character of molar morphology. On all the molars preserved in 47799 and 48404 a small cusp is present near the base of the trigonid on the crest linking the metaconid and a talonid cusp. This cusp is always mesial to the lowest point on the crest and either at the head or just distal to the base of the groove that received the paracone. It is designated the posterior accessory cusp (Mills 1964). None of the molars in the other mandibles of *Peramus*, with the possible exception of the M_1 of M21888, have a posterior accessory cusp.

In comparison to the last premolar of 47739, P_4 of 48404 has a shorter (mesiodistally) posterior basal cusp that is not enlarged into a talonid-like spur, and a larger conical, mesially projecting anterior basal cusp. The protoconid of M_1 exhibits the same lingual flattening found in 47739. Its posterior accessory cusp is low on the slope of the protoconid and set off by a distinct notch from the major distal talonid cusp. A small entoconid is present. Thus, like the first molars of the other group of jaws, the talonid lacks a prominent buccal projection.

The major differences between M_2 and M_3 of 48404 and 47739 are associated with the presence of the posterior accessory cusp on the molars of 48404. On M_2 the cusp is situated low at the base of the trigonid; breakage and distortion of the crown make it appear to be a talonid cusp. Hypoconid and hypoconulid are not so well separated as in 47739 but form a prominent buccal projection mesial and dorsal to the anterior basal cusp of M_3. An entoconid might have been present, but this area is damaged and now covered with preservative. M_3 of 48404 is closely comparable to the M_2. The differences have been described by Mills (*ibid.*).

As now preserved and illustrated by Mills (1964, fig. 1) the talonid of M_4 of 48404 appears to differ significantly from that of 47739, which is essentially unicuspid. On 48404 the distal is the highest talonid cusp. A ridge projecting buccally links it with the posterior accessory cusp, but this ridge is always lower than the apices of these two cusps and might be the result of breakage. A hypoconid could have been present and lost after death. If it was not present the talonid of M_4 would have a structure more closely comparable to the talonid of M_1 than those of M_2 and M_3. M_3 and M_4 are preserved in 47799 and clearly show the presence of posterior accessory cusps on both molars. Although in need of further preparation what is now exposed shows the talonid of M_4 had only one major cusp distal to and separated by a notch from the posterior accessory cusp.

47799 is the only mandible of *Peramus* in which the posteriorly placed dental foramen, the angular process and the base of the condylar process are now preserved. The angle was preserved in the type specimen 47742 and figured by Owen (1871). A small rugose area at the anterior end of the pterygoid fossa might mark the position of a coronoid bone.

e. *Intrageneric Variation*

Noting what appeared to be a relatively wide range in variation in size of the teeth in the mandibles referred to *Peramus tenuirostris*, Simpson (1928, p. 124) concluded two species might be represented. If this proved correct, he suggested 47742 and 48404 would be members of the species with a dentition of larger size. Another suggestion based on considerations of size and various other morphological charac-

ters, was that 47742 and M21888 represented a species distinct from *Peramus tenuirostris* but no formal changes in nomenclature were proposed (Mills 1964). Further preparation of the fossils and additional material has given a slightly better appreciation of variation in size within the sample that in itself does not indicate the presence of two species.

Most other aspects of dental morphology do not clearly indicate heterogeneity of the sample. The exception is the presence or absence of a posterior accessory cusp. It is present on the molars of 48404 (M_{1-4}) and 47799 (M_{3-4}). A posterior accessory cusp might be present on the M_1 of M21888 but the cusp in question is minute and could be the metaconid or a curious individual variation. The talonids of M_2 and M_3 of M21888 are damaged, but if present and as large as those of 48404, some indication of the posterior accessory cusp should be preserved. It is not. Thus the sample can be clearly subdivided on the basis of presence or absence of a posterior accessory cusp, which might indicate taxonomic heterogeneity. Considering the small number of available fossils, we choose to note and describe the variation but not suggest changes in nomenclature.

IV. OCCLUSION AND FUNCTIONAL INTERPRETATIONS

Through the introductory and descriptive sections it has been assumed that M21887 is a maxilla of *Peramus tenuirostris*, a species typified on a mandible. This assumption is justified on the following evidence: M21887, the type, and all other specimens of *P. tenuirostris* came from the Purbeckian Mammal Bed at Durlston Bay. The maxilla is of the proper size to be referable to *P. tenuirostris* and, like the mandible, carries eight postcanine teeth. The upper and lower postcanine teeth exhibit the same pattern of differentiation. The mesial three are clearly premolariform. M^2, M^3, and probably M^4, like M_2 through M_4 are molariform. In both upper and lower dentitions the last premolar is larger than the immediately adjacent premolar and molar and has basal cusps not found on the other premolars. Although molariform, the first molars differ from the others primarily in the absence or small size of primary cusps of the trigon and trigonid. Finally, it will be shown here that when restored the dentition of M21887 is a functional counterpart of the kind of lower dentition on which *P. tenuirostris* was typified.

Because of the lack of extensive wear on the molars of M21887, small size of the fossil, and need to maintain a coat of preservative over fractured areas, wear facets cannot be clearly delimited. This attempt to deduce the functional pattern of the dentition depends primarily on considerations of molar morphology and comparisons with other mammals rather than facets and other direct evidence of wear.

When considered in the context of the work by Crompton and Hiiemäe (1969) on *Didelphis* and studies of various primitive mammals, the morphology of the dentition of *Peramus* suggests that mastication was affected almost entirely by orthal movement of the mandible. A lingual component was introduced during the final stage of jaw closure when the protoconid and parastylar region and/or paracone and buccal wall of the talonid came into contact. The mandibular symphysis of *Peramus* was not fused. The dentition probably was anisognathic and during mastication the animal can be assumed to have alternately employed the right or left side of the dentition.

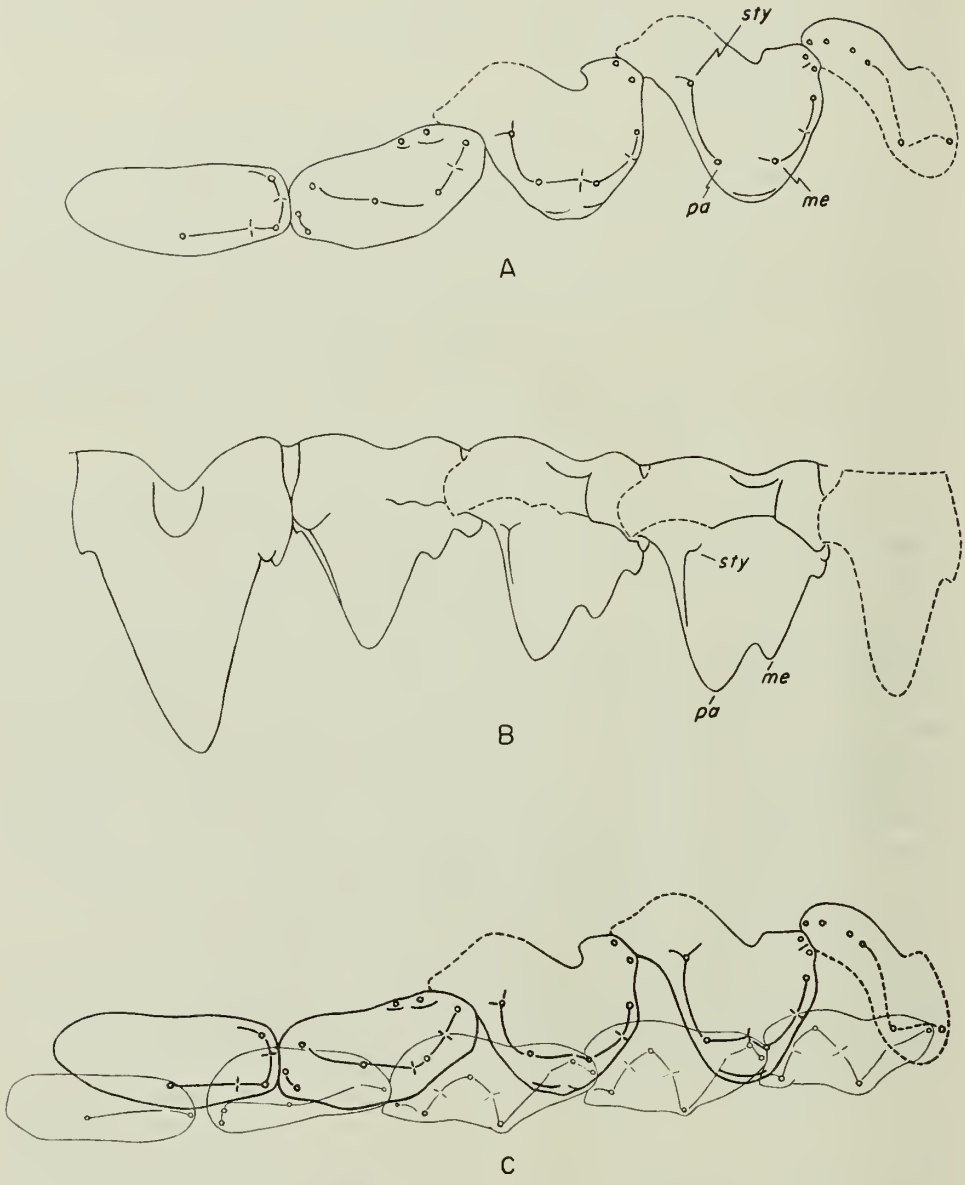

FIG. 2. *Peramus tenuirostris* Owen. Restorations of dentition. P^4 and M^{1-4} in A, occlusal view, and B, labial view. Occlusal relationships of distal premolars and molars near completion of jaw closure in C. (*sty* stylocone; *pa* paracone; *me* metacone.)

No evidence suggests the occlusal pattern of the antemolar dentition differed significantly from the basic therian pattern. The lower canine no doubt occluded just mesial to the upper and the mesial lower premolars lay between the uppers making only limited, marginal contact during mastication.

Although now slightly shifted in position, M^1 having been driven mesially and lingually relative to P^4, clearly these teeth of M21887 were not separated by a deep triangular embrasure like those between adjacent molars (Text-fig. 2). Correlated with the lack of an embrasure is the basically single-cusp morphology of the trigonid of M_1. During the early phase of closure its protoconid was probably received in the valley between the paracone and mesio-lingual cusps of M^1, which in M21887 appears to show traces of wear. When the dentition was fully occluded the protoconid of M_1 appears to have lain distolingual to the point of contact of P^4 and M^1.

The distal crest of the protoconid of M_1 and the crest of its talonid usually form an almost straight line. A buccal salient has not been observed. The paracone of M^1 was received in the groove on the buccal side of M_1 that delimits the talonid and the anterior unit of the crown. A wear facet on the mesial side of this groove is evident on one fossil (facet B, Mills 1964). Apparently the distal crest of the protoconid of M_1, including the metaconid where present, and the mesial crest of the paracone of M^1 formed a functional unit.

The apex of the metacone of a tribosphenic molar is at the junction of two shearing crests. The mesial crest, extending to the base of the paracone, occludes with the crest on the distal slope of the hypoconid. The distal crest forms part of the metastylar blade that occludes with the blade formed by the crest linking the paraconid and protoconid of the distal lower molar.

On M^1 of M21887, between the paracone and the cusp at the disto-buccal corner of its crown, is a large cusp. Its apex is higher than that of the disto-buccal cusp but lower than that of the paracone. In comparison with the paracone the disparity in height is much greater than that of the closely approximated paracone and metacone of M^2 or M^3. The lingual surface of the crown of M^1 just distal to the paracone is not recessed nor are there any traces of wear. The crest linking the distal cusp in question and the disto-buccal cusp of M^1 is blunted and appears to have functioned as a shearing blade acting in conjunction with the crest linking paraconid and protoconid of M_2. The narrow disto-lingual cingulum on M^1 served to deflect food that otherwise would have been driven directly into the gingiva.

Determination of the homologies of the cusp distal to the paracone of M^1 is open to question. The unicuspid talonid of M_1 lacks a hypoconid or other buccal projection. Thus the typical tribosphenic pattern of shear between the distal crest of the hypoconid and mesial crest of the metacone is lacking in the M^1_1 of *Peramus*. This hypoconid-metacone shear pattern is also lacking in *Kuehneotherium*. In this Rhaetic mammal the paraconid, which towered over the talonid of the preceding lower molar, moved upwards to lie between the paracone and "c-cusp" or "metacone" of the upper molar. The talonid of *Kuehneotherium* lower molars is small and usually lacks a buccal salient. Two hypotheses can be offered for the pattern of evolution of tribosphenic molars from those of *Kuehneotherium*. One proposes that in the descendants of *Kuehneotherium* the origin and enlargement of the hypoconid was

coupled with elongation of the talonid, and enlargement and lingual shift of the "c-cusp". Shearing between trigonid and "c-cusp" was limited to the distal face of the latter. The mesial face of the "c-cusp" supported a crest which came to shear against the distal crest of the hypoconid. It follows that the "c-cusp" of *Kuenheotherium* is the precursor of the metacone of tribosphenic molars. Crompton (pers. comm.) has informed us that some lower molars of *Kuehneotherium* have a short buccal salient and on a few upper molars he has observed a small wear facet high on the distal crest of the paracone well removed from the "c-cusp". These observations suggest a second working hypothesis. Origin of the hypoconid and metacone were correlated, the latter arising as the high point of an angulation of the distal crest of the paracone mesial to the "c-cusp". Thus the metacone of tribosphenic molars would be a new cusp and the "c-cusp" might be homologous to the cusp found on the metastylar blade of some primitive tribosphenic molars, the penultimate molar of *Pappotherium* for example.

Because of the inadequacies of the fossil record a decision on the homologies of the cusps distal to the paracone of M^1 of *Peramus* will also reflect a choice between the following alternatives: M_1^1 of *Peramus* are phylogenetically derived from molars that had a hypoconid-metacone shear like that of M_2^2. Or, the ancestors of *Peramus* lacked M_1^1 with a hypoconid-metacone shear and in *Peramus* these teeth are somewhat modified molars of the *Kuehneotherium* functional pattern.

The cusp of M^1 of *Peramus* situated between the paracone and disto-buccal cusp performed a function akin to that of the metacone of a tribosphenic molar in that it was at one end of a buccally directed shearing blade. However, it did not support a mesial crest that sheared against a crest of the hypoconid. Because it did not fully perform the functions of a primitive tribosphenic metacone we prefer not to apply this name. Also the authors cannot agree on whether the "c-cusp" of *Kuehneotherium* can or should be considered the phylogenetic precursor of the distal cusp of the M^1 of *Peramus* or the metacone of tribosphenic molars. We conclude, however, that most probably the ancestors of *Peramus* lacked M_1^1 with a hypoconid-metacone shear (p. 108).

If common features of the occlusal patterns of mammals with tribosphenic dentitions and *Kuehneotherium* can be used to interpret the occlusion of *Peramus*, the stylocone of M^2 and the ridge extending mesially from it should be just buccal to the point where the protoconid of M_2 first contacted the upper molar during closure of the jaws. Because of the curvature of the side of M^2 further closure of the jaws would have required a transverse movement in order to allow the protoconid to slide up the lingual side of the parastylar region. The small size of the stylocone and the ridges radiating mesially and lingually (buccal end of the paracrista) from it and the convexity of the mesial side of the crown of M^2 in this region suggest little shearing occurred here until the protoconid started to slide lingually and dorsally. This moved the crest linking the apex of the protoconid and the base of the metaconid transversely across the nearly vertical segment of the mesial crest (lingual end of the paracrista) of the paracone. The existence of a transverse component of movement is also indicated by the orientation of wear scratches on the M_1 of 47744 (Mills 1964, p. 121).

The metacone of M^2 is situated high on the slope of the paracone. On the lingual surface of the crown a pronounced groove separating the two is directed toward the distal end of the lingual cingulum. This groove received the hypoconid of M_2. Wear facets (facet D) on several M_2's of *Peramus* (Mills 1964, p. 121) demonstrate that shearing occurred between the distal crest of the hypoconid and mesial crest of the metacone. The "lipping" (Mills *ibid.*) produced by the crest on the distal side of the metaconid helped form a long, well-defined groove on the lower molar that received the paracone. As the lower molars were moved dorsally, shearing occurred between the distal crest of the paracone and mesial crest of the hypoconid (note facet C, Mills *ibid.*). Thus, unlike M^1, M^2 exhibits the occlusal pattern of the paracone, metacone, and hypoconid found in tribosphenic molars.

Indications of wear have been found on the lingual surfaces of the talonid and on the crest linking metaconid and hypoconid of several molars of *Peramus* (Mills 1964). None are clearly the result of tooth on tooth contact. If M21887 is a maxilla of *Peramus* and there was not gross individual variation, the molars of *Peramus* lack protocones or other projections that could have produced wear on the lingual surface of the talonid. The top of the talonid crest might have been worn by contact with the lingual cingulum of the opposing molar, possibly acting as a stop to prevent overclosure. The evidence of wear on the lingual side of the talonid is probably the result of abrasion by food.

Because of crushing and distortion, the relative positions of M^2 and M^3 cannot be accurately determined. The distal margin of M^2 has been restored using M^3 as a model. As the relative position of these molars is reconstructed here, the two most disto-buccal cusps are treated as parts of the stylar shelf not directly involved in providing shearing surfaces. The large unnamed cusp between the disto-buccal cusps and the metacone of M^2 was situated mesio-lingual to the point where the protoconid of M_3 contacted the parastylar region of M^3. Shearing might have occurred between the buccal margin of this unnamed cusp of M^2 and the lingual margin of the protoconid of M_3 as the latter was moved lingually and dorsally. The existence of this shearing mechanism is highly speculative.

During closure of the jaws once the trigonids moved lingually and were in position to slip deep into the embrasures between the upper molars, the crest between the paraconid and protoconid of M_3 was positioned to move across the crest between the unnamed cusp and metacone of M^2. This is the typical occlusal relationship found between the metastylar blade and trigonid of tribosphenic molars.

M^3 of *Peramus* appears to have had the same occlusal pattern as M^2:

1. In *Kuehneotherium* an important shearing mechanism involves the entire crest of the ridge linking stylocone and paracone (paracrista) and all of the protoconid-metaconid crest on the distal edge of the talonid. Because of the small size of the stylocone, low buccal end of the paracrista, and convexity of the mesial margin of the crown adjacent to the parastylar region, shearing in this part of the crown of *Peramus* was limited to action between the bucco-mesial margin of the paracone and disto-lingual margin of the protoconid. Although the shearing mechanism was restricted to employ only parts of the crests utilized in *Kuehneotherium*, it does not appear to have been diminished in importance.

2. Functions of the distal crest of the paracone, mesial crest of the metacone, and crests of the hypoconid are those typical of tribosphenic molars.

3. The basal lingual cingulum on the upper molars acted to deflect food away from the gingiva. It might have made contact with the crest of the talonid and served as a stop to prevent overclosure. Evidence of wear on the lingual side of the talonid of the opposing molar is probably the result of abrasion by food, not tooth on tooth contact.

4. A metastylar blade, which functioned with the paraconid-protoconid crest, was formed between the metacone and the unnamed cusp on the distal margin of the crown. The buccal margin of the latter cusp might have been a continuation of the metastylar blade and acted with the lingual edge of the protoconid to produce a shear.

Only the parastylar region of M^4 of M21887 is preserved. It suggests the parastylar regions of M^2 and M^3 could have been large buccal extensions of their crowns each carrying several cusps. On all M_4's of *Peramus* the talonids are essentially unicuspid, but unlike M_1, their crests are directed disto-buccally and form distinct salients. This hypoconid-like projection suggests both a paracone and a much smaller metacone were present on M^4.

The occlusal pattern of *Peramus* exhibits several important differences from those found in mammals with tribosphenic molars. M^2 and M^3 differ in absence of the shearing surfaces associated with the protocone. The small size of the stylocone and paracrista suggest little shearing was effected in this area. Additionally, M^1 and M_1 lacked the interaction of the shearing crests of the paracone, metacone and hypoconid.

V. PHYLOGENETIC RELATIONSHIPS

a. Comparison with *Amphitherium*

Amphitherium prevostii is known from four mandibles discovered in the Stonesfield Slate, a Bathonian (middle Jurassic) unit within the Great Oolite. Maxillae or isolated upper teeth of the species have not yet been found. In most recent studies of Mesozoic mammals *Amphitherium* is classified with the therian mammals and treated as a member or representative of the stock ancestral to *Peramus*, dryolestids, paurodonts*, and mammals with tribosphenic dentitions.

Making use of the morphology and pattern of wear of the lower molars an attempt to reconstruct the upper molars of *Amphitherium* has been made (Text-fig 3, from Mills 1964, p. 125–7). The lower molariform teeth have a basically triangular occlusal outline. The uppers must have had a similar outline but of opposite orientation. When a dentition of this reversed triangular pattern is brought into occlusion the margins of the gingiva at the apices of the embrasures could be damaged by food impacted by the opposing molars. On the lower molars the projecting spur

*The recent study by W. G. Kühne (1968) clearly shows that the concept and content of the Paurodontidae needs thorough review in light of new material from the Jurassic of Portugal. Without attempting to revise the family, for the sake of convenience we choose to employ the Paurodontidae for *Paurodon*, several genera from the Kimmeridgian of Portugal yet to be formally named, *Archaeotrigon*, *Tathiodon*, *Araeodon*, *Pelicopsis*, *Mathacolestes*, and, possibly *Brancatherulum*.

of the talonid protects this part of the gingival margin. No doubt a salient parastylar region with a similar function is present on the upper molars of *Amphitherium.*

The pattern of wear of the trigonids of *Amphitherium* (facets A and B, Mills *Ibid.*) resembles that found on M_2 through M_4 of *Peramus.* A large wear facet (facet C, which is not clearly delimited from facet B on the distal slope of the trigonid) was developed on the bucco-mesial side of the single-cusped talonid. The crest of the talonid is directed disto-buccally and slightly overlaps the trigonid of the following molar. One of the authors (Mills) has re-examined the specimens of *Amphitherium* with improved equipment and finds that the talonid was situated against and largely under the trigonid of the succeeding molar. Where it appears otherwise, this is due to post-mortem displacement. A wear facet along the oblique crest of the talonid (facet F) was interpreted (Mills *ibid.*) to be the result of contact with a lingual cingulum on the upper molar. Evidence from *Peramus*, and other mammals, now indicates contact with a lingual cingulum might have contributed to the wear, but probably facet F is the product of abrasion by food.

As reconstructed (Mills *ibid.*) the upper molars of *Amphitherium* are shown with a prominent lingual cingulum and the metacone situated very near the disto-buccal corner of the crown. These two features of the reconstruction can be modified on the basis of information derived from *Peramus.* Wear on the crest of the talonid (facet F) of *Amphitherium* can be primarily or entirely accounted for through abrasion by food. Probably a lingual cingulum protecting the gingiva is present on the upper molars of *Amphitherium* but it need not be larger than those of *Peramus* or *Kuehneotherium.*

If the apex of the metacone on an *Amphitherium* molar is lower than that of the paracone, and the magnitude of transverse movement slightly greater than previously estimated, the metacone could have been in a much more lingual position than shown in the earlier reconstruction and still produced the facet on the distal end of the talonid (facet D). The wear facet on the distal face of the trigonid (facet B) is larger than that on the mesial (facet A), a relationship similar to that in *Peramus.* This suggests the stylocone and paracrista of *Amphitherium* molars are as small as those of *Peramus.* Thus, within the limits of the available evidence, the upper molars of *Amphitherium* can be reconstructed in a form not greatly different from that of M^2 or M^3 of *Peramus.*

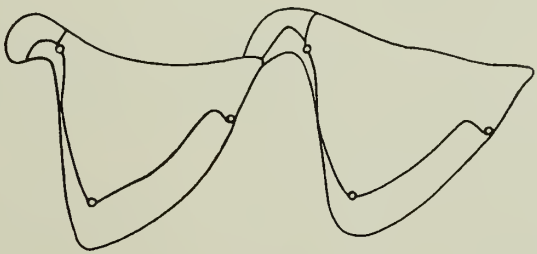

FIG. 3. *Amphitherium prevosti* (H. v. Meyer). Earlier restoration of upper molars (redrawn from Mills 1964, fig. 4B) in occlusal view.

In spite of the possibility of these similarities in upper molar structure and resemblances in the morphology of the lower molars, several features of the dentition of *Amphitherium* suggest it is not directly ancestral to *Peramus*. Like *Amphitherium*, the first molars of paurodonts, dryolestids, and the late Jurassic and younger symmetrodonts do not differ greatly from the second. Usually there are some differences in size—the first molar being smaller—and proportions; but these are not of the magnitude of the differences found between the first and second molars of *Peramus*. We assume that *Kuehneotherium* from the Rhaetic is either a member or representative of the therian radical (Mills 1964; K. A. Kermack *et al.* 1965; D. M. Kermack *et al.* 1968). Information on the morphological differences of its first two molars is not yet available. However, the uniqueness of the degree of morphological difference between the first and second molars of *Peramus* among the probable descendants of *Kuehneotherium* warrants a working hypothesis that this magnitude of difference is not a primitive trait of therians.

M^1 of *Peramus*, except for the small size or absence of the stylocone, closely resembles upper molars of *Kuehneotherium* (note Kermack *et al.*, 1968, Fig. 1). The trigonid of M_1 of *Peramus* does not resemble those of any of the described molars of *Kuehneotherium* but is derivable from them through near or complete loss of the paraconid and metaconid. These changes could reflect a reduction of fully molariform teeth through a pattern of change akin to that involved in the evolution of carnassials in Cenozoic carnivores (Mills *ibid.*, p. 127). In the absence of a hypoconid or buccal salient the M_1 talonid of *Peramus* resembles those of most lower molars of *Kuehneotherium*, not *Amphitherium*. Thus the first molars of *Peramus* are most easily derived from those of a *Kuehneotherium*-type without involving the acquisition and subsequent reduction of the talonid structure found in all molars of *Amphitherium*.

Relative sizes of the distal premolar and mesial molar of *Kuehneotherium* are not certainly known, however, judging from the isolated teeth described by Kermack *et al.* (1968, Fig. 7), the distal premolar could have had a higher crown. The last premolar of the English, late Jurassic symmetrodont *Spalacotherium* is higher than the mesial molar but in at least the lower dentition of *Tinodon* from North America they are of equal height. Among American, late Jurassic dryolestids (Simpson 1929, p. 62) and paurodonts greater crown height of the distal lower and possibly upper premolars appears universal. Of the English representatives of these families *Amblotherium pusillum* contradicts the pattern. Its last lower premolar is higher than the first lower molar, but the inverse proportion characterizes the upper dentition. This evidence suggests another hypothesis: probably greater crown height of the distal premolar relative to the first molar is a primitive therian trait. If so, *Amphitherium* in which the crown of the first molar slightly overtops that of the distal premolar, can be regarded as having diverged from the primitive condition while the lineage leading to *Peramus* did not.

Thus, the simplest interpretation of phylogenetic relationships taking morphology of the distal premolars and mesial molars into account, is that *Amphitherium* and *Peramus* are representatives of disparate lineages. In order to reflect this interpretation we now follow Kermack *et al.* 1968, and others, in removing *Peramus* from the Amphitheriidae and allocating it to a separate family, Peramuridae Kretzoi.

b. Comparisons with Late Jurassic mammals

The work of W. G. Kühne and his associates has produced samples of at least two major Kimmeridgian local faunas from Portugal, here referred to by the names of the principal localities, Guimarota and Porto Pinheiro. Descriptions of these local faunas are just beginning to be published (note Kühne 1968 and refs.; and Krusat 1969), but already several specimens giving evidence pertinent to the ancestry of *Peramus* have been described.

Kühne (1968, p. 121) briefly commented on a mandible containing only P_2 from Guimarota that he identified "cf. *Peramus*". In addition from Guimarota he recovered two isolated lower molars of the size expected for teeth of cf. *Peramus*. Kühne (*ibid.*) comments on the "striking similarity" of these teeth to *Kuehneotherium* and points out several close similarities to *Amphitherium*.

One of us (Clemens) had the opportunity to study these fossils. With a more extensive knowledge of the morphology of *Peramus* it now appears less probable that cf. *Peramus* is part of its ancestry. The gross structure of their dentaries is similar, especially in the size and salient nature of the angular process. However, P_2 of cf. *Peramus* has two small cusps distal to the main cusp while only one is present in *Peramus* and *Amphitherium*. The trigonids of the isolated molars from Guimarota allocated to cf. *Peramus* do not differ significantly from those of M_2 to M_4 of *Peramus*. However, the talonid is unicuspid and "not provided with ridges". Thus it is more closely comparable to the talonids of *Kuehneotherium* and *Amphitherium* than the three or two-cusped, slightly basined talonids of M_2 to M_4 of *Peramus*.

Another fossil pertinent to consideration of the ancestry of *Peramus* is a molar of an as yet unnamed mammal from Porto Pinheiro described by Krusat (1969). The trigonid of this tooth resembles the trigonids of M_2 to M_4 of *Peramus* as well as those of the molars of *Amphitherium* and *Kuehneotherium*. In contrast, the talonid is quite unlike those of any of these mammals. It is large and deeply indented on the labial side. A J-shaped ridge carrying three cusps, originates from the distal slope of the metaconid and forms the lingual and distal margins of this indentation.

Krusat (*ibid.*) rightly points out the uniqueness of the talonid structure of the Porto Pinheiro tooth among molars of Jurassic therians. Only in *Peramus* do some molars also have a three-cusped talonid, but they are incipiently basined and have a distinct crista obliqua. The cusp in the position of a hypoconid at the end of the J-shaped crest on the Porto Pinheiro tooth is by far the lowest of the talonid cusps. Probably this mammal lacked the hypoconid-metacone shear found in some molars of *Peramus* and those of the full tribosphenic type.

It can be hypothesized that in the Porto Pinheiro mammal the paracone supported two long shearing surfaces meeting at a slightly obtuse angle at its apex. Enlargement of the talonid could reflect selection for increase in the size of the paracone and emphasis on this shearing mechanism. The proliferation of talonid cusps might be associated with elaboration of the mechanisms for interlocking adjacent teeth and protection of the gingiva. In any event, if the described tooth is typical of the lower molars of this Porto Pinheiro mammal, it seems unlikely that it is part of the ancestry of *Peramus* in which the evolution of a crista obliqua and lingual basin must have occurred concomitant with enlargement of the talonid.

Brancatherulum tendagurense is based on an endentulous mandible found in the Tendaguru area of Tanzania in the late Jurassic, Upper Saurian Bed. Simpson (1929) suggested *Brancatherulum* is closely allied to *Peramus*. Kühne (1968) noted these two genera are members of a group of eupantotheres including *Amphitherium*, *Archaeotrigon*, and the Kimmeridgian cf. *Peramus* that have a docodontlike angular process of the mandible. Unfortunately the dentition of *Brancatherulum* is unknown and the phylogenetic relationships of the genus remain obscure.

c. Ancestry of *Peramus*, summary

Kuehneotherium from the Rhaetic is considered to be ancestral to or representative of the radical of therian mammals.

Amphitherium from the Bathonian exhibits a grade in evolution of the lower and, we infer, upper molars that probably characterized ancestors of *Peramus*. However, comparison of their distal premolars and mesial molars suggests *Peramus* was not derived from *Amphitherium*. Recently Henkel and Krebs (1969) have adduced evidence suggesting that dryolestids also are not direct descendants of *Amphitherium*. These interpretations suggest, not unexpectedly, that the available collection of Bathonian mammals is a poor sample of eupantotherian diversity at that time.

None of the Kimmeridgian mammals so far described provides compelling evidence for inclusion in the ancestry of *Peramus*. The molars allocated to cf. *Peramus* by Kühne (1968) are more closely comparable to those of *Amphitherium* or *Kuehneotherium*, particularly in structure of the talonid. Cf. *Peramus* could be ancestral to *Peramus* but we feel this conclusion should be treated as one of several working hypotheses until more material becomes available.

Although passing through the evolutionary grade of dental evolution represented by *Amphitherium*, apparently the lineage linking *Kuehneotherium* or a closely related Rhaetic mammal and *Peramus* has yet to be found.

d. Possible descendants of *Peramus*

Most early Cretaceous therians are members of the Spalacotheriidae or Dryolestidae, families established in or before the late Jurassic and certainly not descendants of *Peramus*. The few early Cretaceous mammals that might be derived from *Peramus* are: *Aegialodon* from the English Wealden, the therians of eutherian-metatherian grade from the Trinity Sands including *Pappotherium* and *Holoclemensia*, and *Endotherium*, a poorly known Asian mammal.

Aegialodon is based on an isolated tribosphenic molar from the Cliff End bone bed, a unit of the Wealden, Hastings Beds. In many characters it closely resembles M_2 and M_3 of *Peramus* but there are some distinguishing features. The relative difference in height of trigonid and talonid appears to be less in *Aegialodon*. In both the paraconid is higher than the metaconid but the latter cusp has a slightly more mesial position, relative to the protoconid, in *Aegialodon*. Like at least M_3 and M_4 of *Peramus*, lingual and labial anterior basal cusps (mesial cuspule and mesial ridge respectively of Kermack *et al.* 1965) are present on the molar of *Aegialodon*.

The talonid of *Aegialodon* carries a relatively larger and better delimited basin

than that of *Peramus*. We do not agree with Kermack *et al.* (p. 542, 1965) and Krusat's (1969) suggestions that the crista obliqua of *Aegialodon* is a product of abrasion and Krusat's (*ibid.*) further contention that the structure is not homologous with the ridge linking metaconid and hypoconid found on the molars of various Trinity Sands' therians. Although it was probably accentuated by development of adjacent wear facets, the crista obliqua of *Aegialodon* rises slightly above the lingual talonid facet in a fashion suggesting its eminence is not solely the product of wear.

In *Peramus* the hypoconids of M_2 and M_3 are situated at the apices of distinct buccal salients and are as large or larger than the hypoconulids. A hypoconid-metacone shear was functional. A buccal salient is present on the talonid of *Aegialodon* but two, closely approximated cusps smaller than the hypoconulid are present in the position of the hypoconid. The entoconid of *Aegialodon* is larger and in a more mesial position than that of *Peramus*. Also the talonid basin of *Aegialodon* is larger and is worn in a manner that Kermack *et al.* (1965) thought to be indicative of the presence of a small protocone on the occluding upper molar.

If a lineage derived from *Peramus* was characterized by selection favouring evolution of a protocone, then *Aegialodon* could be its Wealden descendant. Small size and subdivision of the hypoconid is unexpected but the wear facets demonstrate a hypoconid-metacone shear was functional. Although permissive, the evidence supporting the hypothesis that *Aegialodon* is derived from *Peramus* is not compelling.

The Albian therians *Pappotherium* and *Holoclemensia* probably are not descendants of *Peramus* if the hypothesis that *Kuehneotherium* is representative of the therian radical is correct. Upper molars of *Pappotherium* have a large stylocone linked to the paracone by a high ridge, the paracrista. A similar pattern pertains in *Kuehneotherium*. In *Peramus*, however, the labial end of the paracrista is very low and the stylocone minute. An evolutionary pattern involving reduction of paracrista and stylocone and then, subsequently, their enlargement seems unlikely. Although smaller than that of *Pappotherium*, the stylocone of *Holoclemensia* is much larger than that of *Peramus*.

On upper molars of both *Pappotherium* and *Holoclemensia* the protocone and parastyle are linked by a cingulum across the mesial face of the paracone. This cingulum, and the protocone, are probably homologous to part of the mesially continuous lingual cingulum of upper molars of *Kuehneotherium*. In *Peramus* this cingulum is reduced to a short ledge lingual to the paracone and metacone and not continuous across the mesial face of the paracone. Thus, both the small size of the stylocone and lingual cingulum of *Peramus* suggest it is not ancestral to either *Pappotherium* or *Holoclemensia*.

Little can be said about the possibility of direct phylogenetic relationships between the enigmatic Asian *Endotherium* and *Peramus*. In grade of evolution the lower molars of *Endotherium* more closely resemble those of *Pappotherium* than those of *Peramus*. No features of *Endotherium* rule out its descent from *Peramus*, but no evidence strongly suggests this was the case.

In summary, we hypothesize that in the late Jurassic probably there were several peramurid genera. *Brancatherulum* from Africa and cf. *Peramus* from Guimarota could be members of this family. *Aegialodon*, and possibly *Endotherium*, might be

descendants of *Peramus*. Although *Peramus* probably is not their direct ancestor, possibly *Pappotherium* and *Holoclemensia* are descendants of a peramurid having a large stylocone and mesially complete lingual cingulum.

VI. SUMMARY AND CONCLUSIONS

Peramus tenuirostris Owen is represented in the fossil record by only a few fragmentary mandibles and a maxilla. All are from the Purbeckian Mammal Bed, part of the Late Jurassic (Boreal standard) Lulworth Beds of England, and are now in the collection of the British Museum (Natural History).

The dental formula of *Peramus* is $I^{?}_{4}$, C^{1}_{1}, P^{4}_{4}, M^{4}_{4}. Presence of more than four incisors cannot be excluded. In some individuals the large lower canines are supported by deeply scored but probably undivided roots. Of the four premolariform teeth the last, most distal, is distinctly the largest. Neither P^4 nor P_4 is molariform.

M_1, although molariform, is distinguishable from the following molars through absence of a distinct paraconid, small size or absence of a metaconid, and absence of a hypoconid or other buccal projection on the talonid. Likewise M^1 differs from M^{2-3} in its lesser width of crown, relative to length; absence of a cusp with all the functions of a tribosphenic metacone; and lack of a prominent anterior lobe of the stylar shelf.

M_{2-3} are fully molariform tribosphenic molars with three-cusped, imperfectly basined talonids. M^{2-3} have a broad stylar shelf; small stylocone; high, closely approximated paracone and metacone; and narrow lingual cingulum. Unless great individual variation occurred, the upper molars probably lacked a distinct protocone. The morphology of M^4 is unknown. The trigonid of M_4 resembles that of M_3 but the talonid of the last molar is essentially a buccally deflected blade carrying a small entoconid.

All specimens of *Peramus* are allocated to *P. tenuirostris*. The only character suggesting the presence of two species is the regular development of a small cusp, the posterior accessory cusp, on the crista obliqua of the molars of some individuals.

The morphology of its dentition, especially the tribosphenic-like molars, and mandible demonstrate the therian affinities of *Peramus*. We assume that *Kuehneotherium* from the Rhaetic is a member or representative of the therian radical. Also *Pappotherium* and *Holoclemensia* from the Albian are assumed to be representative of therians of eutherian-metatherian grade.

Amphitherium from the Bathonian (Middle Jurassic) has been suggested to be phylogenetically intermediate between *Kuehneotherium* and *Peramus*. The morphologic differences of their distal premolars and mesial molars are interpreted as indicating *Amphitherium* is not directly ancestral to *Peramus*.

Of the Kimmeridgian mammals described by Kühne (1968) "cf. *Peramus*" might be ancestral to *Peramus*, but the evidence is not compelling. If the isolated tooth from Porto Pinheiro described by Krusat (1969) is a typical lower molar of a Kimmeridgian mammal, it is unlikely this mammal is part of the ancestry of *Peramus* in which evolution of the crista obliqua, lingual talonid basin, and encircling cusps must have occurred concomitant with enlargement of the talonid.

Kuehneotherium, *Pappotherium*, and *Holoclemensia* have upper molars with a large stylocone linked to the paracone by a high paracrista and a continuous basal cingulum across the mesial face of the crown. In *Peramus* the stylocone is greatly reduced and the cingulum interrupted. Although Cretaceous eutherians and metatherians probably had a peramurid ancestor, *Peramus* is not a member of this lineage.

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PLATE 1

Peramus tenuirostris Owen

B.M.(N.H.) M21887

FIG. 1. Labial view, left maxilla with P^{1-4} and M^{1-4}. ×25.

FIG. 2. Occlusal view. Heavily damaged lingual section of M^4 outlined but not shaded. ×25.

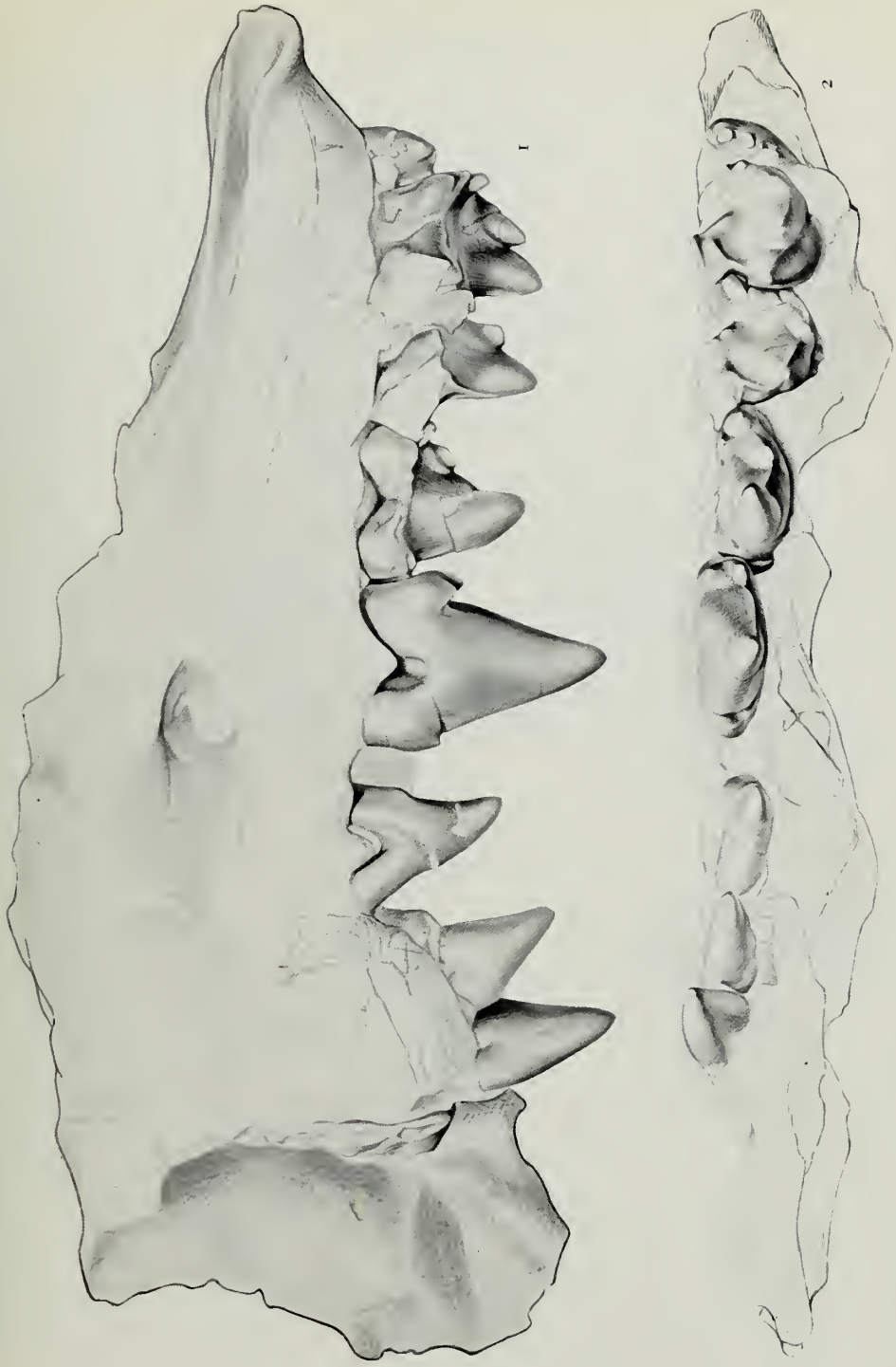
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PLATE 2

Peramus tenuirostris Owen

B.M.(N.H.) M21887

FIG. 1. Lingual view, left maxilla with P^{1-4} and M^{1-4}. ×25.

FIG. 2. Oblique view across labial fragment of M^4, and crowns of M^3 and M^2. ×25.

FIG. 3. Cross-section through base of crown of M^2 to show development of lingual cingulum. ×25.

FIG. 4. Cross-section through base of crown of M^3 to show development of lingual cingulum. ×25.

1
2
3
4

PLATE 3

Peramus tenuirostris Owen

B.M.(N.H.) 47739

FIG. 1. Occlusal view of canine alveolus, P_{1-4} and M_{1-4}. ×25.

FIG. 2. Lingual view with outline of mandibular ramus. ×25.

1

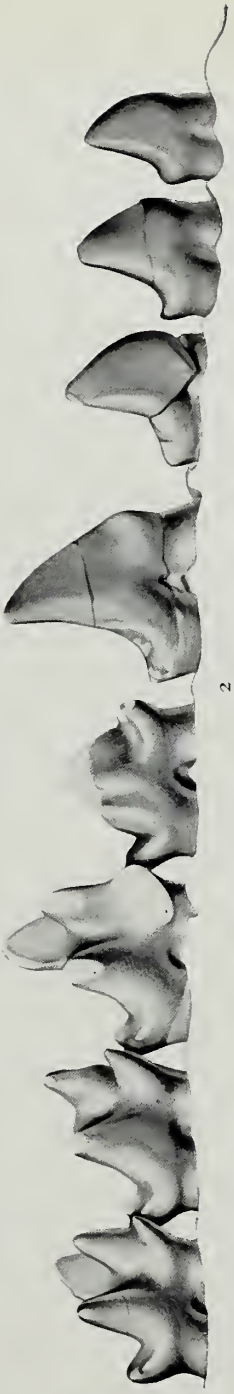

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PLATE 4

Peramus tenuirostris Owen

B.M.(N.H.) 47739

FIG. 1. Labial view of a section of mandibular ramus containing canine alveolus, P_{1-4} and M_{1-4}. ×25.